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Temporal expectancies driven by self- and externally generated rhythms

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Abstract

The dynamic attending theory proposes that rhythms entrain periodic fluctuations of attention which modulate the gain of sensory input. However, temporal expectancies can also be driven by the mere passage of time (foreperiod effect). It is currently unknown how these two types of temporal expectancy relate to each other, i.e. whether they work in parallel and have distinguishable neural signatures. The current research addresses this issue. Participants either tapped a 1Hz rhythm (active task) or were passively presented with the same rhythm using tactile stimulators (passive task). Based on this rhythm an auditory target was then presented early, in synchrony, or late. Behavioural results were in line with the dynamic attending theory as RTs were faster for in- compared to out-of-synchrony targets. Electrophysiological results suggested self-generated and externally induced rhythms to entrain neural oscillations in the delta frequency band. Auditory ERPs showed evidence of two distinct temporal expectancy processes. Both tasks demonstrated a pattern which followed a linear foreperiod effect. In the active task, however, we also observed an ERP effect consistent with the dynamic attending theory. This study shows that temporal expectancies generated by a rhythm and expectancy generated by the mere passage of time

can work in parallel and sheds light on how these mechanisms are implemented in the brain.

Keywords: Rhythmic tapping, crossmodal, entrainment, oscillation, temporal expectation

Introduction

Making temporal predictions is central to our everyday life. To hit a tennis ball we need to accurately predict when the ball will arrive. Otherwise the action will result in a swing and a miss. Two sources of information that humans can use to generate temporal expectancies are the sense of elapse of time and, if available, rhythm. There is evidence that humans and animals are capable of using both these sources (see Nobre and Rohenkohl, 2014 for review). Although it is evident that the two types of temporal expectancy generation are not mutually exclusive, it is currently unknown how they relate to each other, i.e., whether or not they work in parallel and have distinguishable neural signatures. The current research addresses this issue.

The sense of elapsed time has been shown to be involved in generating expectancies about upcoming events, the control of actions, and the inference of causality (Gallistel and Gibbon, 2000; Janssen and Shadlen 2005). One way to create temporal expectancies is using a warning signal indicating that an event is about to occur. The time interval between the warning signal and the impending stimulus is also known as the foreperiod. Varying this time interval has shown to affect behaviour, such as increasing the foreperiod leads to faster response times (Niemi and Näätenen, 1981). The foreperiod effect is typically explained by the fact that the likelihood of the occurrence of a conditional event that has not yet occurred increases with time. This probability of increased expectancy is driven by

the Hazard function (Janssen and Shadlen 2005; Luce 1986). For example, the likelihood that the traffic light will turn green increases the longer you wait.

On the other hand, rhythms, if available, provide additional information compared to the mere lapse of time when generating temporal expectancies. Many events in our environment follow a rhythmic pattern. Evidence of how rhythms form temporal expectations comes mainly from rhythmic cueing experiments (and, thus, concerns external rhythms). For example, Jones et al. (2002) presented participants with a standard tone at the start of a trial and a comparison target tone at the end of the trial. The participants' task was to judge if the two tones had the same pitch. Sandwiched between these two tones was a task irrelevant rhythm. Importantly, the comparison tone could be presented in synchrony, or slightly too early or too late compared to the rhythm. The accuracy of judging the pitch was best when the comparison tone was in synchrony with the rhythm and tailing off either side in an inverted U-shaped pattern. The dynamic attending theory was suggested to explain these results (Jones, 1976; Jones, 2010).

The dynamic attending theory proposes that rhythms entrain periodic fluctuations of attention which modulate the gain of sensory input (Large and Jones, 1999). A large number of studies support this notion. First, similar to the results from Jones et al. (2002), presenting stimuli in synchrony with a rhythm has been shown to improve choice response times (Martin et al., 2005), detection thresholds (Herrmann et al., 2016; Lawrance et al., 2014), and perceptual discrimination (Rohenkohl et al., 2012). Second, more recently, evidence in line with dynamic attending also comes from research showing that intrinsic neural oscillations can entrain to external rhythms by aligning the firing pattern of neurons

with rhythms in our environment (Lakatos et al., 2008; Arnal & Giraud, 2012; for reviews see Calderone et al., 2014; Henry and Herrmann, 2014). Finally, perception of near threshold visual (Bush, Dubois, VanRullen, 2009) and auditory stimuli (Henry and Oblesser, 2012) has been shown to be influenced depending on where in the phase of the neural oscillation the stimulus falls (see VanRullen, 2016 for a recent review). Synchronous vs. asynchronous presentation of stimuli has also been shown to influence various EEG components such as N1 (e.g., Escoffier et al., 2015), N2 (Doherty et al., 2005), and P3 (Breska and Deouell, 2014; Doherty et al., 2005; Correa and Nobre, 2008; Rohenkohl and Nobre, 2011). As with external events, many actions are also rhythmic (such as running, walking, or speech) and the regularities of these human activities are typically in the seconds time-scale below 4Hz (Arnal et al., 2015; Keitel et al., 2017). There is evidence to suggest the motor system is imperative in generating temporal predictions which shape perception (Grahn and Rowe, 2012; Schubotz, 2007, Morillon et al., 2015). For example, there is a strong link between the auditory and motor systems, in particular in relation to rhythms (for recent reviews see Ross and Balasubramaniam, 2014; Ross et al., 2016; Lima et al, 2016). Movements, such as tapping have been shown to influence the perception of temporal information and improving temporal sensitivity (Iordanescu et al., 2013; Manning & Schutz, 2013). Morillon et al. (2014) showed a benefit of target processing when participants were tapping along to a beat compared to passive listening to the same beat. Further, Nozaradan et al. (2015) showed that tapping to music involves two distinct types of entrainment: neural entrainment to the auditory rhythm underlying beat processing, and a distinct neural entrainment to movement which underlies the production of synchronized movements. What is less well understood is whether self-generated rhythms in the absence of external

auditory cues also entrain neural oscillations and how stimuli in and out of phase with this rhythm are processed.

The current study aims to investigate how rhythmic entrainment influences perceptual and behavioural processes by using both externally induced as well as internally generated rhythms within the seconds time-scale (here around 1Hz), which is commonly observed in everyday rhythmic actions (Arnal et al,. 2015; Rose et al., 1994; Buhusi and Meck, 2005). The aforementioned two types of temporal expectancy should yield dissociable result patterns. Contrary to the inverted U-shaped pattern observed in rhythmic cueing studies, the foreperiod effect typically results in shorter response times for longer foreperiods, suggesting a greater response preparation with increasing probability of occurrence of the stimulus (see Nobre et al., 2007; Niemi and Näätenen, 1981 for reviews), as well as attenuated N1 at longer compared to shorter foreperiods (Correa and Nobre, 2008). The inverted U-shaped and the linearly increasing pattern of results are thus indicative of the two types of temporal expectation, respectively. The present study adapted the paradigm used by Jones et al. (2002, described earlier). Participants performed a pitch judgement task but instead of being presented with a sequence of tones, they tapped a rhythm and a comparison target was then presented in synchrony, earlier, or later than the self-paced tapping (active task). In a second task, exactly the same rhythm was presented back to the participant using tactile stimulators (passive task). The first objective of the study was to investigate whether or not self-paced tapping and external tactile rhythms entrain slow wave delta oscillations. Second, we aimed at testing the effect of external and internal rhythmic entrainment on auditory stimulus processing as measured by means of reaction times/errors and ERPs. There were two possible outcomes, both of which might be

observed but at different processing stages. A.) Any processing that is driven by the passage of time, should show a pattern of results corresponding to a foreperiod effect. For example, decreasing attenuated sensory components for late compared to in synchrony and also early stimuli. B.) Any processing that is driven by the rhythm should show a pattern in line with the dynamic attending theory, e.g., enhanced components in synchrony compared to early and late stimuli. To foreshadow the results, in the condition with internally generated rhythms we observed two separate ERP effects consistent with the foreperiod effect and dynamic attending theory, respectively.

Methods

Participants

Twenty-one paid participants took part in this study (2 were removed due to excessive artefacts and 1 due to excessive errors in the rhythm task, the experiment being prematurely aborted for this participant). There were 11 male and 7 female participants, all right handed, with a mean age of 26.4 years. Ethical approval for the study was granted by the Comité de Protection des Personnes (CPP) Ile de France II. All participants provided written informed consent.

Stimuli and apparatus

Stimulus presentation was controlled using E-Prime (Psychology Software Tools, Inc.) on a computer which also sent markers to a second computer recording EEG, using PyCorder (Brain Products GmbH.). Tactile stimuli were presented using a round solenoid (15 mm in diameter) driving a magnet (1.5 mm in diameter) to the finger pad of the right index finger. Every time a current is passed through the solenoid the magnet made contact with the

finger. The solenoid was mounted in a foam square to minimize any sound from the stimulator if in direct contact with the table. The tactile stimulator was connected to a custom built tactile controller (Heijo Research Electronics), which in turn was connected to the stimulus presentation computer. Each tactile stimulus presentation was 150 ms long, creating the sensation of a single tap.

Tones were created using Audacity®. All tones were 150 ms long with a 5 ms rise and fall time. The following 17 tone frequencies were used: 440.00, 442.55, 445.11, 447.69, 450.28, 452.89, 455.52, 458.16, 460.81, 463.48, 466.16, 468.86, 471.58, 474.31, 477.06, 479.82, and 482.60 Hz. The difference between each tone on the scale was 10 cents (a semi-tone which are the adjacent black and white keys on a piano, is 100 cents, an octave is 1200 cents). Standard tones were in the range of 452.89 and 468.86 Hz. Comparison tones could be 50 cents higher or lower compared to the standard. Comparison tones spanned the whole range of 17 tones. Tones were presented in stereo via headphones at 60dB SPL.

A dynamic staircase was used in the experiment to keep accuracy of tone discrimination between 60-80%. Each task started with a difficulty of discriminating between standard and comparison tone of 50 cents (level 1). The hardest discrimination was at level 5, where the difference between the standard and comparison tone was 10 cents. The difficulty level was adjusted according to the performance level over the previous 10 trials. When the participant's accuracy was higher than 80% then the difference between the standard and comparison decreased from 50 to 40 cents, and further down to 30, 20, and 10 cents. When the accuracy fell lower than 60% the task became easier as the standard and comparison

tone difference increased by 10 cents. There was a minimum of six trials between each change.

A monitor was used to present a black fixation cross on a white background. Participants responded using two keys ('0/Ins' and './Del') on a numpad, with their left hand. This numpad was situated to the left of the participant. Participants pressed the downward arrow on a separate keyboard to tap a rhythm using their right index finger. The downward arrow of the keyboard (active task) was situated on the table in front of the participant, in a straight line behind the central fixation cross. The tactile stimulator (active task) was situated in the same place as the downward arrow so that the participant's right index finger was placed in the same location for the active and passive tasks.

Design and procedure

The study consisted of two tasks, active tapping task and passive tactile stimulation task. Each task included the Factor Time with three levels; early, in synchrony, and late.

The experiment in short; participants heard a tone, and then tapped a key four times after which a second tone was presented. Their task was to discriminate whether the two tones were of the same or different pitch. The second tone was presented in or out of synchrony with the participant's rhythm in that particular trial; however, this temporal manipulation was not related to the task as such. In the passive task, they judged whether the two tones were the same or different and in between they were presented with four taps to their index finger.

Active tapping task

The participants started with the active task. Each trial started with "New trial" presented in the centre of the monitor for 300 ms and then replaced by a fixation cross which was present throughout the trial. After 1500 ms the standard tone was presented for 150 ms. The participant then tapped a rhythm of exactly 4 taps with their right index finger, approximately 1 tap every second. After the last tap, a second 150 ms comparison tone was presented either in or out of synchrony with the participant's rhythm (see Figure 1). The participant's task was to indicate, by pressing one of two keys with their left hand, whether the second comparison tone was the same or different pitch compared to the first standard tone. Thus, the task was not related to the rhythm. The response keys were counterbalanced across participants. The fixation cross stayed on screen until the participant made a response. If the participant was incorrect in discriminating whether the two tones were the same or not, error feedback (*Error*) was presented on screen for 1000 ms. An additional 100 ms inter-trial interval was added before a new trial.

Catch trials were trials when the standard tone was presented, followed by four taps, but no comparison tone was presented. No response was required and the next trial started after 2000 ms.

The comparison tone was either presented in or out of synchrony with the participant's own rhythm in each trial. A tone out of synchrony was either presented early or late, according to the average rhythm in that trial. The tones were equally likely to be early, in synchrony, or late. To calculate *when* to present the comparison tone, the average rhythm was calculated in a trial (the mean interval between tap 1-2, 2-3, 3-4). A comparison tone in

synchrony was presented with the average rhythm after the onset of the 4th tap. A comparison tone presented in the early condition was based on one fifth subtracted from the average rhythm (early = average – average/5). That is, if the average rhythm was 1000 ms then the comparison tone in the early condition would be presented 800 ms after the last tap. In the late condition, 1/5 of the average rhythm was added to the interval between last tap and tone presentation. The minimum average rhythm allowed was 800 ms, or an error message "Too fast" appeared. Within these parameters, the shortest possible interval between the last tap and an early comparison tone would be 640 ms. If the rhythm was too irregular (average standard deviation of rhythm > 80 ms), an error message "Too irregular" appeared. If they pressed the key a fifth time, thus a fifth tap in the rhythm, an error message "Only four taps" appeared. If they conducted any of these three errors the trial was terminated and the same trial started again.

The active task consisted of 6 blocks in total with 40 trials per block. In total the active task included 240 trials with 72 early, 72 in synchrony, and 72 late targets. The probability of the three conditions was 1/3. 24 trials were catch trials where no comparison tone was presented. For half of trials the comparison and standard tone were the same and for half they were different (25% of trials were higher and 25% lower). The probability of the early, in synchrony, and late stimuli occurring was 0.3 each and the probability of a catch trial occurring in a trial was 0.1. The Hazard rate function (Luce, 1986) is the probability that an event will occur at a particular time, divided by the probability that it has not yet occurred, prior to each of the four possible events. The probability that the event would occur was: p=0.3 for early, p=0.43 for synchrony, p=0.75 for late targets, and p=1.0 if it was a catch trial.

Passive tactile task

In the passive task participants did not tap their rhythm but were instead presented with 4 taps between the two tones. The presentation of the taps to the right index finger was the exact rhythm which the participant had generated in the previous block thus providing identical rhythms in both tasks. The only difference between tasks was that no error message related to rhythm ("too fast", or "too irregular", or "too many taps") was presented. The same number of blocks and error free trials were used in the passive task as in the active task. Tones were randomly presented and each participant started with discrimination at level 1 (50 cents) in the passive task as well.

The behavioural analysis included response time (RT) and accuracy (% correct pitch discrimination) data and were submitted to an ANOVA with the factors Time (early, in synchrony, late) and Task (active, passive). Analysis of RTs included correct target discrimination trials only and responses below 1500 ms.

Electrophysiological recording and analyses

Electroencephalogram (EEG) was recorded from 64 scalp locations (ActiCAP, BrainProducts GmbH). Amplifier bandpass was 0.1-200 Hz and digitisation rate was 500 Hz, online referenced to FCz. EEG analysis was conducted using Brain Vision Analyzer (BrainProducts GmbH). After recording, the EEG was digitally re-referenced to a common average.

Oscillation analysis locked to last tap

To visualize the 1 Hz oscillation throughout the trial, the data was first epoched into 8000 ms time periods starting 5000 ms before and 3000 ms after the last tap/tactile stimulation

in the rhythm, thus the full length of a trial. Each 8000 ms long epoch was bandpass filtered between 0.5 Hz and 1.5 Hz using a second order Butterworth filter in the forward and reverse directions (Figure 3A waveforms). Oscillatory analysis was performed on all electrodes on 5000 ms segments centred around 3000 ms before and 2000 ms after the last tap. That is, the segment was focused on the interval of the trial where rhythmic activity would be expected; ignoring the beginning (up until the first tap) and end (after the response had been made) intervals of the trial.

A Fast Fourier transform (FFT) using Hanning windowing (10%) was implemented on the normalized data[1] of the 5000 ms long epoch for the frequency range 0.5-50 Hz. Spectra were created for each single trial and subsequently averaged. The frequency resolution of the FFT was 0.12 Hz. Electrode C3 was selected for further statistical analysis. C3 is contralateral to the right hand and is the electrode location where both passive somatosensory (e.g. Jones and Forster, 2014) and active rhythmic tapping (e.g., Nozaradan et al., 2015) effects are commonly observed.

The average tapping frequency across all 18 participants was 1.085Hz with a range of 0.89-1.16Hz. The fastest frequency which could be tapped, without producing an error message, was 1.25Hz. To account for the 1/f bias the tapping frequency bin (0.98-1.1Hz) was compared to the average power (μV) of neighbouring frequencies (0.73-0.85Hz and 1.34-1.46Hz) for electrode C3. The data was analysed using a 2x2 ANOVA with the Factors Frequency (central tapping, average of neighbouring frequencies) and Task (active, passive).

[1] Normalization: Each spectral line value in the entire segment is divided by the value of the total area of the spectrum within the 0.5-50Hz frequency range and multiplied by 100. As a result, a relative distribution of the individual spectral lines is provided, allowing to compare changes in the relative spectral distribution across segments and channels.

Comparison tone locked ERPs

To investigate the effects of entrainment of neural oscillations on perceptual processes we specifically explored the auditory N1-P2 complex (Key et al., 2005) previously shown to be modulated by rhythmic cueing (Sanabria and Correa, 2013) and self-initiated sounds (Timm et al., 2014). The N1 peak latency is commonly observed around 100 ms and P2 approximately 175 ms after stimulus onset (Wood & Wolpaw, 1982; Woods, 1995; Tremblay et al., 2001). Data was epoched into 600 ms periods starting 100 ms prior and 500 ms post to stimulus onset. Baseline correction was performed on the 100 ms interval prior to stimulus onset for each segment (the average of the points in the interval was calculated, and this was subtracted from all points in the epoch). Baseline correction was applied to all channels in the data set. Trials with artefacts (voltage exceeding ±100μV relative to baseline, at any electrode) were removed prior to EEG averaging. Epochs were averaged separately for early, synchrony, and late conditions. Comparison tone locked ERPs are presented with a low-pass filter of 30 Hz for visual presentation purposes (Figure 5 A).

To investigate the N1-P2 complex, two successive time intervals were analysed; 98-138 ms and 144-204 ms (see Figure 4A for topographical maps of each time interval). The first interval was centred on the peak of the N1 (118 ms, averaged across all conditions) and a 40 ms interval was selected based on similar studies investigating effects of temporal attention on auditory N1 processing (90-130 ms: Lange et al., 2006; Lange, 2012; Lange and Röder, 2006; Sanders and Astheimer, 2008). Analysis of the second time interval followed the N1 window whilst not overlapping and was centred on the peak of the P2 (174 ms, averaged across all conditions).

Three regions were analysed: Anterior (AF3, AF4, F1, Fz, F2), Central (FC1, FC2, FCz, C1, C2, Cz, CP1, CP2, CPz), and Posterior electrodes (P1, P2, Pz, PO3, PO4, POz) (see electrode map in Figure 4B). In each region left, medial, and right electrodes were pooled together to create the factor Laterality to investigate the effects in respect to the electrode midline (Lange and Schnuerch, 2014). For each region a repeated measures ANOVA was conducted including the Factors Task (passive, active), Time (early, synchrony, late), and Laterality (left, medial, right), and to explore whether any effect was driven by conditional probability or rhythmic expectation, a linear and quadratic trend analysis was performed using within-subjects contrasts. Where the assumption of sphericity was violated Greenhouse-Geisser adjusted probability and degrees of freedom are reported.

Standard tone locked ERPs

To explore any general effect of Task the same time intervals and regions included in the comparison tone analysis (above) were used to analyse ERPs time locked the standard tone. Only the factors Task (passive, active) and Laterality (left, medial, right) were included.

Results

Behavioural results

The behavioural analysis of response times (RTs) included correct target discrimination trials only and responses below 1500 ms (2.75% of RTs were above 1500 ms). Behavioural RTs compared early, synchrony, and late conditions for each Task.

RTs (ms) and accuracy (% correct pitch discrimination) were submitted to an ANOVA with the factors Time (early, in synchrony, late) and Task (active, passive).

RT analysis showed a significant main effect of Time ($F(2,34)=3.59$, $p=.039$, $\eta^2_p=.17$) and trend analysis showed this effect was quadratic ($F(1,17)=7.14$, $p=.016$, $\eta^2_p=.30$) and not linear ($p=.29$, $\eta^2_p=.07$). In synchrony targets (667 ms, SD - 79.0) were faster than early (686.4 ms, SD - 76.7) and late targets (677 ms, SD – 87.1) (see Figure 2). There was no main effect of Task ($p=.48$, $\eta^2_p=.03$) or Task*Time interaction ($p=.25$, $\eta^2_p=.08$).

Analysis of accuracy data showed no effect of Time ($p=.14$, $\eta^2_p=.11$), Task ($p=.54$, $\eta^2_p=.02$), or Task*Time interaction ($p=.20$, $\eta^2_p=.09$).

The average tapping frequency was 1.08Hz. The average time interval between taps was 925 ms (SD- 37 ms) which led to the average interval between the last tap and early targets being 742 ms, in synchronous targets 927 ms[2], and late targets 1108 ms. The interval between the standard tone and the first tap was 841 ms on average, calculated from standard tone onset to first tap onset. Exactly the same timings were presented in the passive task. In the active task, participants could make errors based on their rhythmic tapping accuracy, in which case they had to re-do the trial. Participants' tapped "Too fast" or "Too irregular" on average 2.8% and 5.4% of trials, respectively. The error message "Only four taps" occurred on average less than 0.001% of trials.

Oscillation results

The oscillation analysis indicated that there is a 1 Hz oscillation triggered by both tasks (Figure 3). A 2x2 ANOVA with the factors Frequency (central tapping, average of neighbouring frequencies) and Task (active, passive) showed a significant effect of

[2] The discrepancy of 2 ms between tapping frequency and the average in synchrony condition is due to rounding effects

Frequency ($F(1,17)=7.88$, $p=.012$, $\eta^2_p=.32$) with a larger amplitude for the central tapping frequency (0.29 μV) compared to the average of the lower and higher neighbouring frequencies (0.21 μV) (see Figure 3 C). There was no main effect of Task ($p=.16$, $\eta^2_p=.12$) or Frequency*Task interaction ($p=.33$, $\eta^2_p=.06$).

Standard tone locked ERPs

There were no effects of Task[3] or Task*Laterality interaction in any of the three analysed regions for the 98-138 ms (all p's>.12, $\eta^2_p<.14$) or 144-204 ms time intervals (all p's>.14, $\eta^2_p<.11$).

Comparison tone locked ERPs[4]

[3] Main effect of Task in the 98-138 ms interval for: Anterior - $F(1,17)=2.68$, $p=.12$, $\eta^2_p=.14$; Central $F(1,17)=.23$, $p=.64$, $\eta^2_p=.01$; and Posterior electrodes - $F(1,17)=.22$, $p=.65$, $\eta^2_p=.01$.
Main effect of Task in the 144-204 ms interval for: Anterior - $F(1,17)=.05$, $p=.82$, $\eta^2_p=.003$; Central - $F(1,17)=.002$, $p=.97$, $\eta^2_p<.001$; and Posterior electrodes - $F(1,17)=.19$, $p=.67$, $\eta^2_p=.011$.

[4] To simplify the presentation of results we have not included the effects of Laterality in the main text. There was a main effect of Laterality over anterior electrodes in the 98-138 ms time interval ($F(1.4,23.1)=15.60$, $p<.001$, $\eta^2_p=.48$). Trend analysis revealed a significant quadratic trend ($F(1,17)=94.49$, $p<.001$, $\eta^2_p=.85$) with larger negative amplitude for medial (-3.03 μV) compared to left (-2.41 μV) and right (-2.32 μV) electrodes. Over posterior electrodes there was a significant main effect of Laterality ($F(2,34)=4.04$, $p=.027$, $\eta^2_p=.19$) and Task*Laterality interaction ($F(1.4,24.6)=6.95=p=.008$, $\eta^2_p=.29$). Follow-up analysis for each task separately showed no effect of Laterality in the passive task ($p=.051$, $\eta^2_p=.18$) whilst a Laterality effect in the active task ($F(1.4,24.6)=5.53$,$p=.017$, $\eta^2_p=.25$). Trend analysis revealed a quadratic trend ($F(1,17)=14.61$, $p=001$, $\eta^2_p=.46$) with larger positive amplitude for left and right electrodes (0.94 μV and 1.0 μV respectively) compared to medial electrodes (0.70 μV).

In the 144-204 ms time interval there was a Laterality*Time interaction ($F(4,68)=3.78$, $p=.008$, $\eta^2_p=.18$) at anterior electrodes. Follow-up analysis for left, medial, and right electrodes separately showed no effect of Time (all p's>.17, $\eta^2_p<.10$). At central electrodes there was main effect of Laterality ($F(2,34)=14.06$, $p<.001$, $\eta^2_p=.45$) and a Laterality*Time interaction ($F(4,68)=3.33$, $p=.015$, $\eta^2_p=.16$). Follow-up analyses showed no effect of Time over left electrodes ($p=.27$, $\eta^2_p=.08$) or medial electrodes ($p=.056$, $\eta^2_p=.17$) but an effect of Time at right electrodes ($F(1.5,25.2)=7.43$, $p=.006$, $\eta^2_p=.30$). Polynomial contrasts showed this effect was linear ($1,17)=9.25$, $p=.007$, $\eta^2_p=.35$). No other significant effects including Laterality and Time were observed. Taken together, the central linear effect on the slope of the N1 was more right than left of the midline. Over posterior electrodes there was a main effect of Laterality ($F(2,34)=26.45$, $p<.001$, $\eta^2_p=.61$). Trend analysis showed a significant linear ($F(1,17)=19.48$, $p<.001$, $\eta^2_p=.53$) as well as quadratic trend $F(1,17)=35.27$, $p<.001$, $\eta^2_p=.68$) with left electrodes showing smallest positive amplitude (1.07 μV) compared to right (1.46 μV) and medial electrodes (1.67 μV).

98-138 ms interval

There was a main effect of Task over anterior electrodes ($F(1,17)=7.24$, $p=.015$, $\eta^2_p=.30$) with larger negative amplitude in the active compared to passive task (-2.73 µV and -2.44 µV respectively). There was no effect of Task over central ($p=.51$, $\eta^2_p=.03$) or posterior electrodes ($p=.48$, $\eta^2_p=.03$) and no Time or Task*Time interaction for analysis of the anterior ($p=.33$, $\eta^2_p=.06$ and $p=.34$, $\eta^2_p=.06$ respectively) and central regions ($p=.43$, $\eta^2_p=.04$ and $p=.34$, $\eta^2_p=.06$ respectively). Over the posterior region there was a Task*Time interaction ($F(2,34)=4.23$, $p=.023$, $\eta^2_p=.20$). Follow-up analyses for each task separately showed an effect of Time in the active task ($F(2,34)=3.81$, $p=.032$, $\eta^2_p=.18$) with a significant linear trend ($F(1,17)=7.32$, $p=.015$, $\eta^2_p=.31$) whilst no quadratic trend ($p=.52$, $\eta^2_p=.02$). There was no effect of Time in the passive task ($p=.52$, $\eta^2_p=.04$).

144-204 ms

Anterior electrodes. There was no effect of Task ($p=.49$, $\eta^2_p=.03$), Time ($p=.38$, $\eta^2_p=.06$), or Time*Task interaction ($p=.10$, $\eta^2_p=.13$).

Central electrodes. Analysis of the central regions showed a main effect of Time ($F(1.4,23.6)=3.91$, $p=.048$, $\eta^2_p=.19$) and polynomial contrasts showed this effect was linear ($F(1,17)=4.75$, $p=.044$, $\eta^2_p=.22$) and not quadratic ($p=.56$, $\eta^2_p=.02$) (see Figure 5A. & B., top). There was no Task ($p=.51$, $\eta^2_p=.03$) or Time*Task interaction ($p=.60$, $\eta^2_p=.03$) effect.

Posterior electrodes. There was a main effect of Time ($F(2,34)=4.73$, $p=.015$, $\eta^2_p=.22$) and also Time*Task interaction ($F(2,34)=4.28$, $p=.022$, $\eta^2_p=.20$). Each task was analysed

separately. In the passive task there was a significant effect of Time ($F(2,34)=3.80$, $p=.032$, $\eta^2_p=.18$) and trend analysis confirmed this effect was linear ($F(1,17)=6.64$, $p=.020$, $\eta^2_p=.28$) and not quadratic ($p=.64$, $\eta^2_p=.01$). In the active task there was an effect of Time ($F(2,34)=5.39$, $p=.009$, $\eta^2_p=.24$) and contrast showed a significant quadratic ($F(1,17)=16.4$, $p=.001$, $\eta^2_p=.44$) whilst no linear trend ($p=.74$, $\eta^2_p=.007$) (see Figure 5A. & B., bottom). There was no main effect of Task ($p=.24$, $\eta^2_p=.08$).

Discussion

Most reactions to external stimuli and most actions meant to achieve effects in the environment are dependent on the timing of events in the surroundings. The ability to implicitly or explicitly use this timing is, thus, essential for humans and animals to efficiently interact with their environment. Yet, although temporal expectations have indeed been shown to influence neural processing (Nobre et al., 2007; Morillon and Schroeder, 2015), less research has been dedicated to the investigation of how movement-related temporal expectations are established and affect subsequent processing. The present study addressed this question.

We used a tapping task as a very simple form of behaviour inducing temporal regularities. As action-related processing comprises an efferent and an afferent component that can be isolated, we studied a condition in which temporal expectation is induced by tapping actions, comprising both efferent and afferent processing, as well as a condition in which it is induced by afferent processing only. To be more precise, we investigated how self-generated rhythms and the same rhythms externally induced by a tactile stimulator entrain neural oscillations and influence processing of auditory stimuli presented in or out of

synchrony with the rhythm. The first objective was to determine whether self-paced finger tapping actually entrains neural oscillations. The frequency data presented in Figure 3 suggests 1 Hz oscillation triggered by both tasks, which might represent spontaneously occurring neural oscillations aligned by phase resetting to the structure of rhythmic stimulation (Canavier, 2015). This is in line with findings that low-frequency oscillation can entrain to the rhythm of the stimulus stream, resulting in increased response gain for sensory inputs arriving during high-excitability phases (Lakatos et al., 2005, 2008; see Schroeder and Lakatos, 2009 for a review). Although there was no significant Task*Frequency interaction, a review of Figure 3 suggests the observed entrainment of oscillation effect at 1 Hz is stronger in the active compared to the passive task. This may be due to different demands in the two tasks. There is evidence to suggest a greater neural synchrony, predominantly in motor areas, for internally compared to externally generated rhythmic movement (Serrien, 2008; Gerloff et al., 1998). Serrien (2008) proposed that self-paced tapping results in a general intensified demand of temporal processing when external cues are unavailable. The second objective was to investigate the effect of active and passive rhythmic tapping on the processing of auditory stimuli. In the active task, we found an ERP effect on the P2 component consistent with the dynamic attending theory. Moreover, in both tasks, there was a temporal expectancy effect relating to elapsed time before the auditory comparison tone.

In the active task a temporal expectancy effect was demonstrated as an inverted U-shaped pattern of results at posterior areas with smaller P2 for in synchrony compared to out of synchrony targets. The effect is thus in line with the dynamic attending theory suggesting that entrainment to the temporal structure of events optimize the processing of an

expected forthcoming stimulus. Our experiment is the first to show this effect for self-generated tapping sequences. The effect demonstrated attenuated ERPs for in synchrony targets compared to early and late targets. There have only been a few studies which have explored temporal orienting effects on the auditory P2. Contrary to the present effect of temporal expectancy at posterior electrodes, Sanabria and Correa (2013) found an enhanced P2 for in compared to out of synchrony tones based on a preceding rhythm. However, Schafer et al. (1981) found a larger P2 potential in the condition where no temporal information was available compared to when a tone appeared in synchrony with the beat. Recently, Fitzroy and Sanders (2015) found a larger P2 for auditory tones which appeared at a weak (unattended) compared to strong (attended) metric beat with a similar time interval (150-190 ms) and posterior topography of the effect (although this was the case in a musicians group only; in a non-musician group the effect was reversed). The present study confirms these latter results.

A bit earlier, in the N1 interval there was a main effect of Task at anterior electrodes with a larger N1 in the active compared to the passive task for the comparison tone. This may reflect the increased attention required in the more demanding active task. This main effect may relate to the suggestion that attention and temporal expectancy are independent mechanisms (Derosiere et al., 2015; Summerfield and Egner, 2009). Interestingly, there was no such task difference when the same analysis was applied to the standard tone at the start of the trial. This suggests there was not a general difference in attentional set between tasks, but instead, the attentional demands differed after the rhythm and when the comparison tone was being processed. Future research may wish to orthogonally investigate attention and temporal expectancy following active and passive rhythms.

Furthermore, in the N1 time interval, for the comparison tone, there was also evidence of a process relating to the foreperiod effect. Here, around 100 ms post tone onset, there was a linear decrease in amplitude from early to late targets. This effect was only present in the active task and over the posterior region. In the following time interval (144-204 ms) the same foreperiod effect was present in both tasks at central electrodes (see Figure 5). Note that, as concerns this effect in the N1 range, the expected event is attenuated, just as was the case with the effect in the P2 range. However, here the expectation is not based on rhythm but on elapsed time. ERP waveforms visually suggest this central effect best be viewed as a continuation of the effect on the downward slope of the N1 (see Figure 5). Indeed, the P2 is often referred to as the N1/P2 complex as the two share many characteristics (Key et al., 2005) and effects on the N1 and P2 often follow each other in paradigms exploring auditory stimuli following an action (e.g., Timm et al., 2014; Horváth et al., 2012; Schafer & Marcus, 1973). However, the P2 has also been dissociated experimentally from the N1 (Crowley & Colrain, 2004) and the scalp distribution of the P2 is less localised than the N1 (Näätenen, 1992). These results suggest some stages of stimulus processing to be modulated by the temporal expectancies related to the passage of time, with the probability of the occurrence of the event growing over time (Neimi and Näätenen, 1981).

Our findings are consistent with a model proposed by Lange (2013). This model differentiates between temporal orienting due to the task-relevance of events at different time points, which is supposed to enhance N1 amplitudes, and orienting due to the expectation that an event occurs at a particular time point, which is supposed to decrease N1 amplitudes. Concerning the latter process, the model proposes the greater the stimulus

probability the more attenuated the effect on the N1 and stimulus processing ERPs (see also Shafer et al., 1981; Clementz et al., 2002). In the present study early, in synchrony, and late comparison tones were equally likely to occur. However, recalculating the probability rate in terms of conditional probability expectation (Hazard rate – see methods section) a negatively skewed distribution that the target will appear is observed (p=.3, p=.43 and p=.75, for early, synchrony, and late targets respectively). This pattern order is also observed for the downward slope of the N1 in the present study suggesting early processing is driven by a mechanism determining the expectation that an event occurs at a particular time point based on the elapsed time.

Taken together the two patterns of results we observed have a number of implications. They show that temporal expectancies generated by a rhythm and expectation generated by the mere passage of time are dissociable, as they seem to affect different stages of stimulus processing. They show that the two expectancy processes are not mutually exclusive, as they both occur in the same trials. They also show that the conditional probability expectation affects processing earlier than the expectation based on rhythm, in this case in the active task only. Furthermore, it should be noted that both types of expectation carry valuable and correct information. To expect incoming information based on the self-generated rhythm is useful in the current experiment as it helps processing the input (tactile notably) triggered by all the taps of the sequence. The effect observed in the current experiment shows simply that this expectation continues for at least one more cycle after the tapping stopped. At the same time, the test stimulus was presented before, at, or after the expected (based on the rhythm) time point. As a consequence, expecting the tone

as a function of the lapse of time optimises stimulus processing in the current study as well since it reflects the probability of stimulus occurrence.

There was a behavioural effect whereby participants were significantly faster responding to comparison tones which were in synchrony with their rhythm compared to when presented early or late across both tasks, although, the effect was visibly more pronounced in the active compared to passive task (Figure 2). This pattern is consistent with the dynamic attending theory which proposes benefits of stimuli presented in compared to out of phase with a rhythm (Jones, 2010; Large and Jones, 1999). Faster response times for synchronous compared to asynchronous targets agrees with previous research using both visual (Doherty et al., 2005), auditory (Sanabria et al., 2011), and crossmodal audiovisual stimuli (Bolger et al., 2013). However, there was no benefit of tone discrimination accuracy in the synchronous compared to asynchronous conditions. This was at first an unexpected result as the task emphasis was pitch discrimination accuracy and not speeded responses. Therefore, the accuracy data did not replicate that of the original study by Jones et al. (2002) or similar studies (Jones et al., 2006 and Herrmann et al., 2016) (although see Bauer et al., 2015 for failure to replicate the original Jones and colleagues (2002) expectancy profile). There are several methodological differences which limit direct comparison between the original and present study. For one, the active task was essentially a dual task (active tapping together with pitch judgement). Moreover, in addition to different attentional demands, the two task may have evoked functionally dissociable timing processes. It has been proposed that finger tapping (the active task) elicits explicit timing (Zelaznik et al., 2002) as the participants required to overtly estimate durations (to tap rhythmically within a standard deviation of 80 ms). The passive task elicited implicit timing

as the rhythm was a by-product to the task. Explicit and implicit timing have been proposed to be dissociable processes with discrete neural substrates (see Coull and Nobre, 2008 for a review). Importantly though, the task at hand, to judge the pitch of the auditory tone was identical in both tasks and did not rely upon timing. Note that the behavioural response time, and accuracy effect, did not differ significantly between tasks. The current finding shows that the temporal expectation induced by the rhythm played a role in both tasks, although the effect is more pronounced in the active task. The fact that, in the ERPs, we found the U-shaped pattern of results only in the active task suggests that the effect in the range of the P2 reported above unlikely directly translate into clear behavioural differences. Future research should try to establish a more direct link between observed brain activity and behaviour.

The work here also adds important theoretical contributions to the growing literature investigating how external rhythms are entrained and influence stimulus processing across modalities. Several recent studies have shown crossmodal effects of rhythmic entrainment using audiovisual (Escoffier et al., 2015; ten Oever et al., 2014; Jones, 2015; Brochard et al., 2013; Escoffier et al., 2010) and visuotactile stimuli (Keil et al., 2017). Lakatos et al. (2007) demonstrated that tactile input re-sets the phase of ongoing neural oscillations in auditory cortex in non-human primates. The present behavioural results in the passive task statistically follow the dynamic attending theory proposing that rhythmic fluctuations of attention should be formed independently of the stimulus modality. However, the descriptive data (Table 1 and Figure 2) suggests the significant behavioural effect is largely driven by the active task indicating further research on audio-tactile entrainment of neural oscillations is required to more conclusively establish this crossmodal link in humans. The

ERP pattern in the passive task followed the temporal expectation based upon conditional probability. Future research may wish to vary the conditional probability of the target to isolate effects based upon rhythmic expectation and conditional probability (see Cravo et al., 2011, for similar manipulation using a single event cue).

Taken together the present study suggests that self-paced tapping and externally generated rhythms entrain neural oscillations. Behavioural results followed the dynamic attending theory as, overall, responses to in synchrony targets were faster than out of synchrony targets. Auditory ERPs showed evidence of two distinct temporal expectancy processes. Both tasks demonstrated a pattern which followed a linear foreperiod effect. However, in the active task, we also observed an ERP effect consistent with the dynamic attending theory. This study shows that temporal expectancies generated by a rhythm and expectancy generated by the mere passage of time can work in parallel and sheds light on how these mechanisms are implemented in the brain.

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Figure captions

Figure 1. Schematic representation of events in an Active and Passive task trial. The order of events in a trial was the same in both tasks. However, the *Tap* refers to the keypress in the active task. In the passive task, the *Tap* refers to a tactile tap presented to the participant using a tactile stimulator. The variable SOA was based on the average interval in that trial and refers to either early, in synchrony, or late condition. After the comparison tone the fixation cross stayed on screen until the participant had responded. If they were incorrect they received an Error message on the screen for 1000 ms.

Figure 2. Response times (in milliseconds) to auditory targets for the Active (dark grey bars) and Passive task (light grey bars). There was a significant quadratic effect of Time as in synchrony targets were faster compared to when targets were presented early or late across both tasks. This is represented by the thin solid trend line. Error bars are standard error of the mean.

Figure 3 A. The waveforms **s**how 1Hz filtered data (0.5-1.5 Hz) in the Active (left) and Passive (right) tasks for electrode C3. The X-axis represents time and 0 ms is centred at the last (4th) tap of the rhythm. Thus, the comparison tone would be presented at around 1000 ms. Lines represent early (black), synchrony (red), and late (blue) conditions. **B.** The corresponding spectral frequency plot for C3 for the Active (left) and Passive (right) tasks where the X-axis represents frequency (0.5-10Hz) and Y-axis is amplitude measured in μV. The central tapping frequency points to the average tapping frequency which was 1.08Hz in both tasks. The topographical maps show the FFT of the three bins used for analysis (measured in μV). That is, 0.98-1.1Hz represents the topography for the average tapping frequency (middle map). The top (0.73-0.85Hz) and bottom topography (1.34-1.46Hz) represents the neighbouring bins used in the analysis. **C.** Bar graph of the

amplitude for C3 representing the central tapping frequency (green - 0.98-1.1Hz) and the average of neighbouring frequencies (blue - 0.73-0.85Hz and 1.34-1.46Hz). There is a significant main effect with larger amplitude for the central (green) compared to neighbouring frequencies (blue). Error bars are standard error of the mean.

Figure 4 A.*:* Topographies of the analysed time intervals (98-138 ms and 144-204 ms) presented separately for each task (active and passive) and condition (early, in synchrony and late). Topographical maps are measured in μV (N1: -4.0 – 4.0μV and P2: -2.0 – 2.0μV). **B.** The electrode selection used for analysis of anterior, central and posterior regions as well as pooled electrodes for left, medial, and right. Note, AFz (black electrode) was the ground and part of analysis.

Figure 5 A.*:* Grand average ERP waveforms for targets presented early (black), in synchrony (red), and late (blue) in the active (left column) and passive tasks (right column). ERPs are time locked to auditory target onset (time 0 ms) and including 100 ms baseline correction interval. ERP waveforms represent pooled electrodes over central (FC1, FC2, FCz, C1, C2, Cz, CP1, CP2, CPz) and posterior areas (P1, P2, Pz, PO3, PO4, POz). **A*. (top):*** Over central electrodes there was a linear effect of Time in both tasks in the 144-204 ms time interval. **A. *(bottom):*** There was a posterior effect of Time in the 144-204 ms time interval which was different in the active and passive task. In the active task there was a curvilinear effect as out of synchrony tones showed a larger positivity compared to in synchrony targets. In the passive task there was a linear effect. **B. (top):** Average amplitude for early, in synchrony, and late targets across both tasks and all central electrodes in this time interval. The topographical map in the top right shows the difference between early and late targets, averaged across both tasks**. B. (bottom):** Average amplitude for early, in synchrony, and late targets for each task separately and averaged across all posterior electrodes. In the 98-138 ms time interval (bottom left) there was a significant linear effect in the active task (red bars) – represented by the dashed trend line. In the 144-204 ms interval (bottom right), there was a significant quadratic trend in the active task (dashed trend line) and linear trend (solid trend line) in the passive task (grey bars). All topographical maps represent the 144-204 ms time interval and measured on the same scale (-0.60

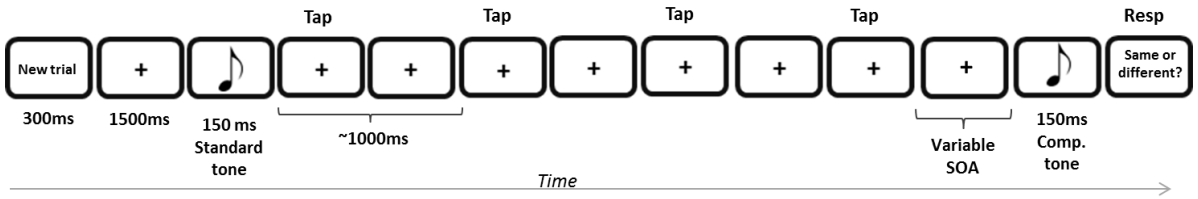
– 0.60 μV). Error bars are standard error of the mean and y-axes show amplitudes of ERPs in microvolt (μV).

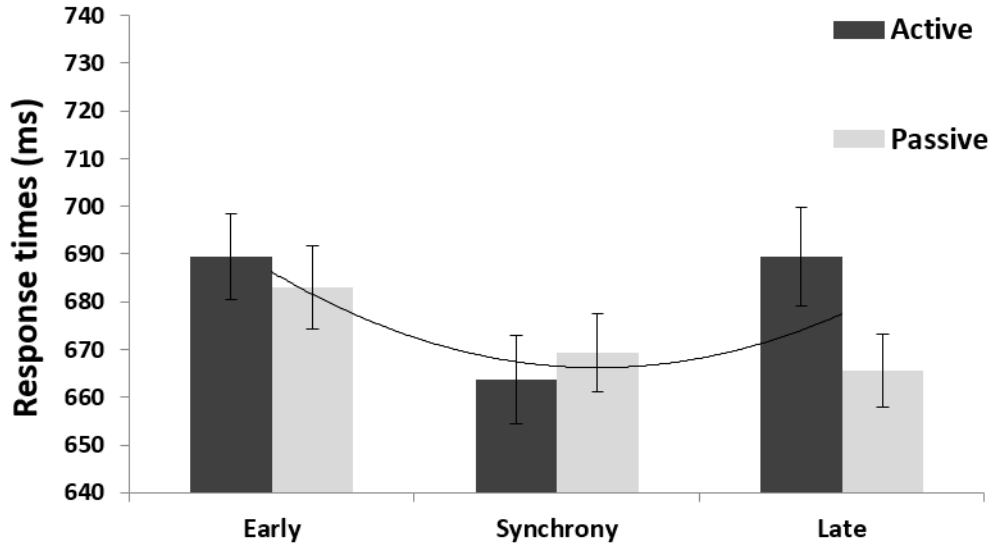
Table 1. Average response times (RTs) in milliseconds with standard deviations (SD) for early, in synchrony and late targets, presented separately for the active and passive task. Accuracy represents correctly judging the pitch of comparison tone measured in per cent (%). Overall score is average of both tasks together.

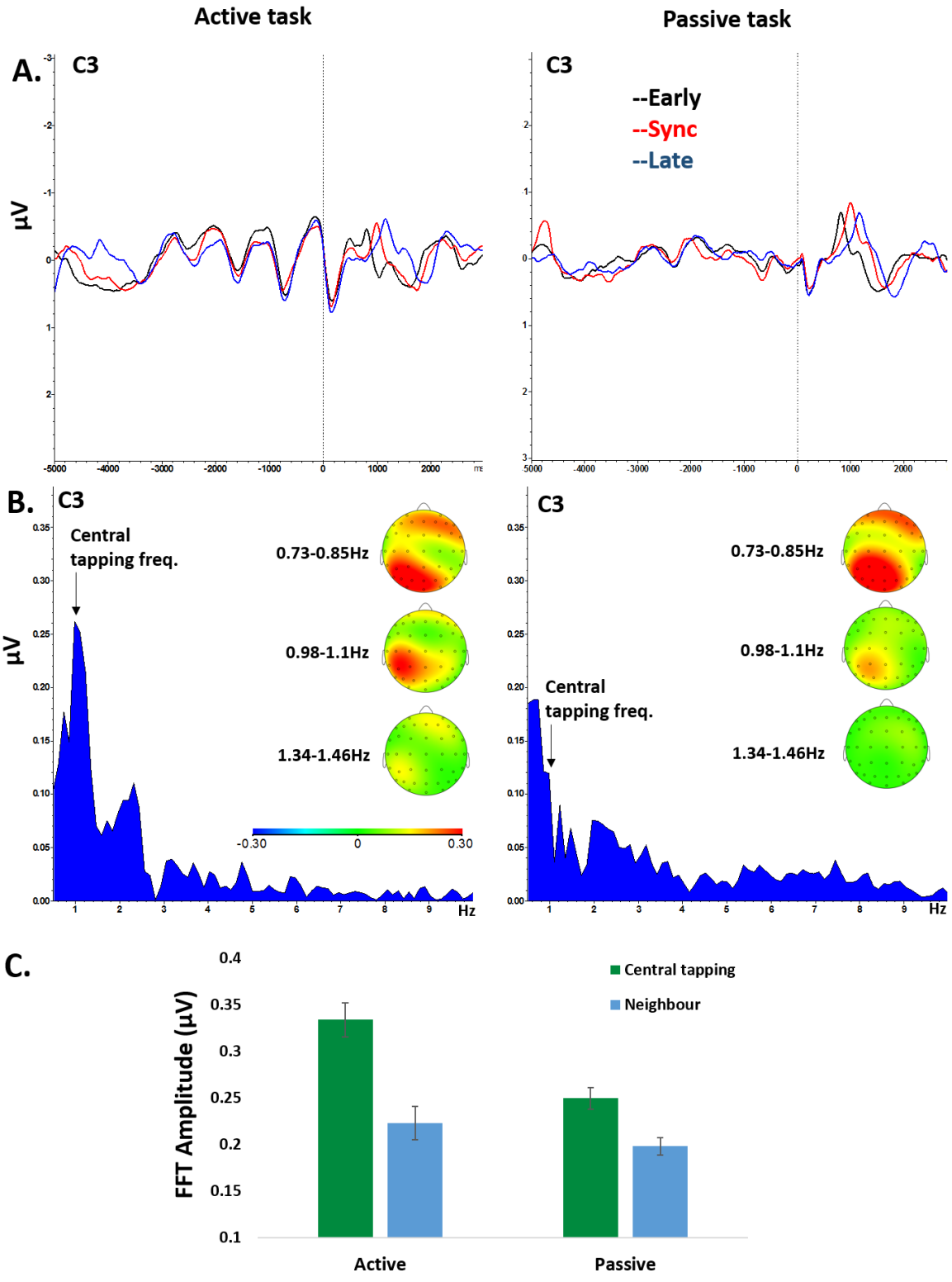
	Active		Passive		Overall	
	RT (SD) in ms	**Acc. (SD) in %**	**RT (SD) in ms**	**Acc. (SD) in %**	**RT**	**Acc.**
Early	689.4 (76.7)	72.29 (5.0)	683.1 (74.2)	74.37 (3.5)	**686.2**	**73.33**
In sync.	663.7 (79.0)	73.04 (6.0)	669.3 (69.1)	70.4 (4.6)	**666.5**	**71.72**
Late	689.4 (87.1)	71.2 (4.7)	665.5 (64.6)	70.5 (4.0)	**677.5**	**70.85**

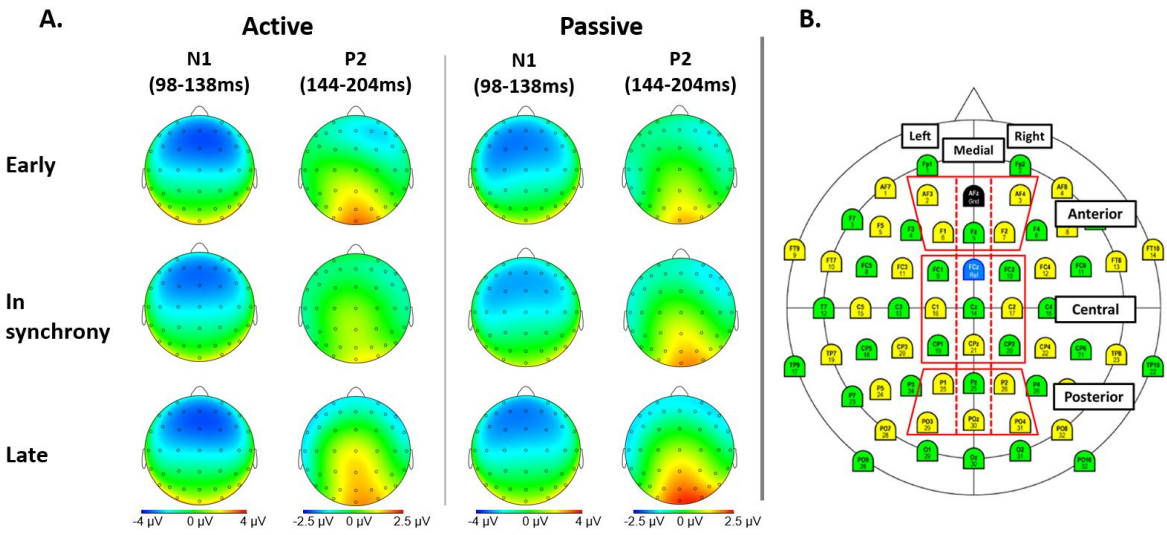
Highlights:

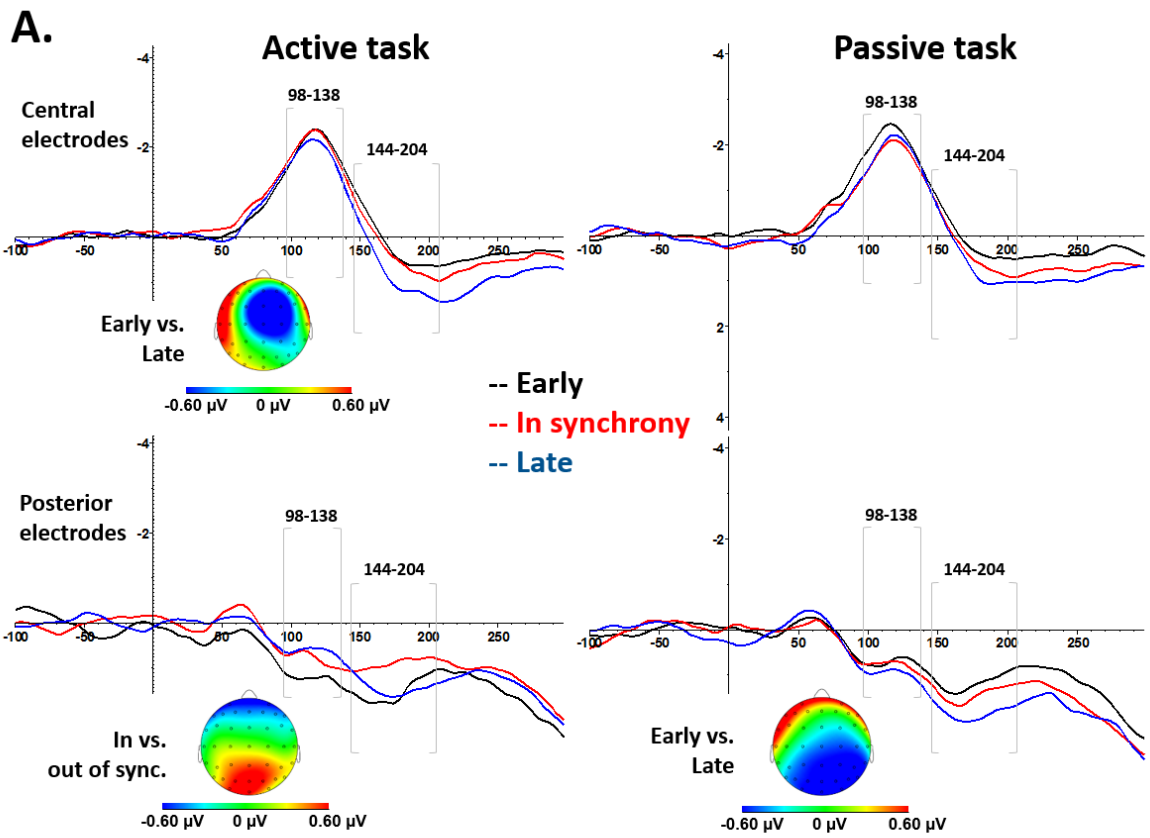
Temporal expectancies can be driven by rhythms or by the mere passage of time
We conceived a paradigm using EEG that tests for both these forms of expectancy
We compared self-generated and externally generated rhythms
We found evidence for both expectancy processes working in parallel

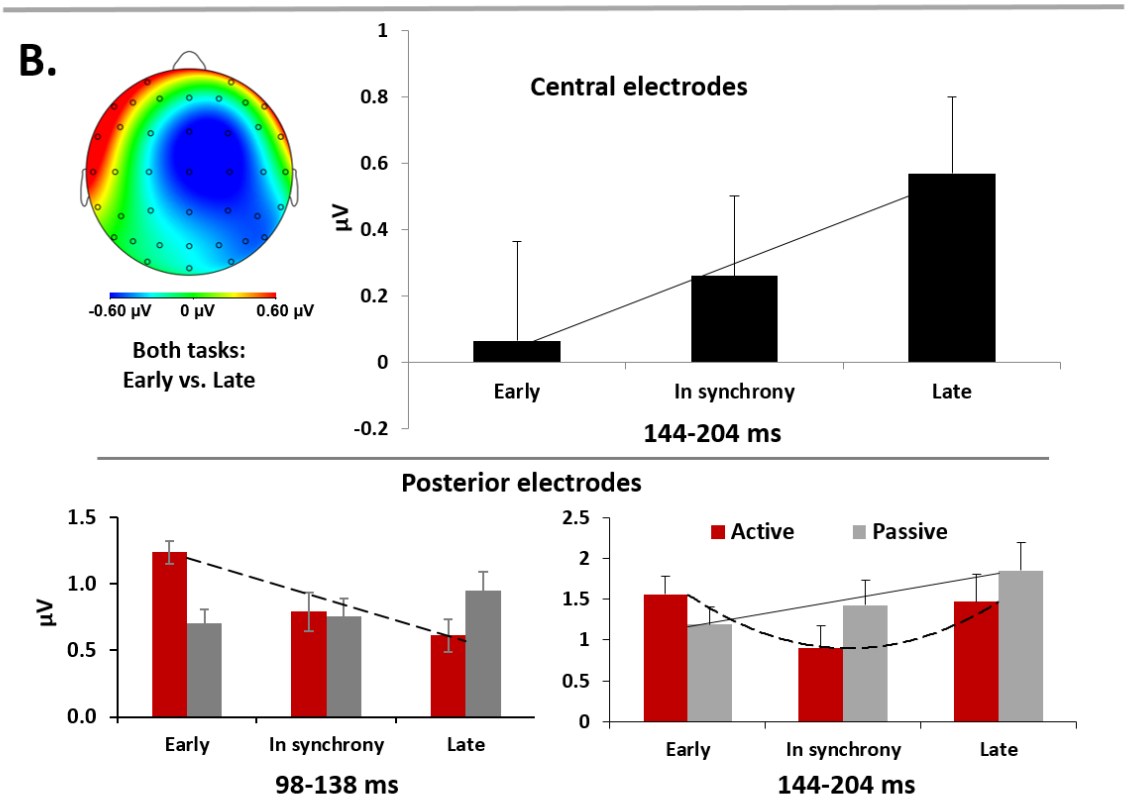









A.
Active task
Passive task
Central electrodes
98-138
144-204
Early vs. Late
-0.60 µV 0 µV 0.60 µV
-- Early
-- In synchrony
-- Late
Posterior electrodes
In vs. out of sync.
Early vs. Late


B.
-0.60 µV 0 µV 0.60 µV
Both tasks: Early vs. Late
Central electrodes
µV
Early
In synchrony
Late
144-204 ms
Posterior electrodes
98-138 ms
Active
Passive
144-204 ms